Eye colour variation in Rufous-bellied Tit Melaniparus rufiventris in western Tanzania

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Received 25 August 2014

Summary.—I report records of pale-eyed Rufous-bellied Tits *Melaniparus rufiventris* ssp. from western Tanzania, including sight records and a specimen in the Museum für Naturkunde, Berlin, from Kakoma, one of three *M. r. pallidiventris* syntypes located, for which the previously overlooked eye colour is recorded as yellow-white. Pale eye coloration has never previously been documented in *pallidiventris*. I also describe several minor plumage differences from birds east of the central Tanzanian rift (also considered to be *pallidiventris*) and provide evidence that pale-eyed and dark-eyed adults co-occur within the same population to the west. I conclude that the range of *M. r. masuknensis* probably extends to south-west Tanzania and that differences between eastern and western Tanzanian specimens assigned to *pallidiventris* may warrant separation at subspecific level through resurrection of *M. r. rovumae*, collected in eastern Tanzania and since subsumed in *pallidiventris*. However, given the small sample size of western Tanzanian birds (due to the paucity of museum specimens), I recommend waiting for more data, including phylogenetic comparison of the *rufiventris* complex as a whole.

The taxonomic status of the Rufous-bellied Tit *Melaniparus rufiventris* complex is controversial, being currently considered to comprise between three and five taxa. Fry *et al.* (2000) recognised only *M.* (then *Parus*) *r. rufiventris* (Bocage, 1877), *M. r. pallidiventris* (Reichenow, 1885) and *M. r. masukuensis* (Shelley, 1900), considering all three to be conspecific. Harrap & Quinn (1996) also recognised *M. r. diligens* (Clancey, 1979) and *M. r. stenotopicus* (Clancey, 1989), and followed Sibley & Monroe (1990) in separating the three western forms (*rufiventris*, *diligens* and *masukuensis*) as Rufous-bellied Tit from the two eastern taxa (*pallidiventris* and *stenotopicus*) as a separate species, Cinnamon-breasted Tit, based primarily on iris coloration (pale in western taxa, dark in eastern forms) and plumage (belly orange in western forms, paler cinnamon in taxa). Dowsett & Dowsett-Lemaire (1993: 369) recognised just one species, noting records of potential hybrids where the two forms meet, a lack of data from potential hybridisation zones and the argument that 'iris colour is not necessarily a biological isolating mechanism'.

Recently, Johansson *et al.* (2013), as well as placing all African tits in the genus *Melaniparus*, sampled three specimens from the *rufiventris* group; a *M. r. rufiventris* (= *diligens*) at the Naturhistoriska Riksmuseet, Stockholm (NRM 570164) collected in Namibia, and one each at the Museum of Vertebrate Zoology, Berkeley (MVZ uncatalogued, RCKB1104) and Museums of Malaŵi, Blantyre (MOM 2007.2.228), both of which they ascribed to *M. r. pallidiventris*. However, collecting locality (Ntchisi Forest, Central Region, Malaŵi; *cf.* Dowsett-Lemaire & Dowsett 2006), eye colour (cream; R. Bowie *in litt.* 2014) and plumage coloration confirm these specimens to be *masukuensis*, not *pallidiventris*. The genetic distance between the Namibian *rufiventris* (= *diligens*) specimen and the Malaŵian *masukuensis* is fairly short, as expected for conspecific taxa. Two other molecular phylogenies of titmice (Gill *et al.* 2005, Tietze & Borthakur 2012) claim to have sampled *pallidiventris*, a specimen at the Museum of Comparative Zoology, Cambridge, MA (MCZ



Figure 1. Atlas data for *M. r. rufiventris* and *M. r. pallidiventris* in Tanzania and adjacent countries. Diamonds = masukuensis, triangles = western pallidiventris / masukuensis, circles = eastern pallidiventris. Star indicates erroneously labelled White-bellied Tit *M. albiventris* (FMNH 216938). Question marks indicate data deficient regions. Mid grey indicates distribution of major areas of miombo woodland mapped at broad scales by White (1983).

279710). Given the collecting locality (Mzimba District, Northern Region, Malaŵi) and plumage coloration in photographs, this specimen is also *masukuensis* not *pallidiventris*. This means that no specimens of *M. r. pallidiventris* have been genetically sampled to date. In the absence of such data, given the findings described below, I choose not to treat *rufiventris* and *pallidiventris* as separate species.

Distribution

According to atlas data (Baker & Baker in prep.) and all other literature, the only taxon known to occur in Tanzania is dark-eyed M. r. pallidiventris (including the synonym rovumae). In eastern Zambia, west of the Albertine / Tanganyika Rift, the taxon involved is pale-eyed M. r. masukuensis, which Dowsett et al. (2008) suggested shows 'perhaps a slight approach to the even paler M. r. pallidiventris (with eye brown, rather than yellowish) in parts of the east.' Tanzanian pallidiventris is split into two apparently separate populations, east and west of the Gregory Rift (hereafter 'eastern' and 'western Tanzania'; Baker & Baker in prep.), with the western population apparently contiguous with masukuensis in Zambia, and the eastern population possibly contiguous with pallidiventris in Mozambique and Malaŵi, although no atlas data are available for northern Mozambique. The three known syntypes for pallidiventris were collected by Böhm in 1881, at Kakoma, west of the Gregory Rift, and described by Reichenow in 1885, seven years before Shelley described rovumae, 1892, from the Rovuma River, east of the Gregory Rift, which is now a synonym of pallidiventris. Fig. 1 shows the current distribution in Tanzania and adjacent countries. In Malaŵi only pallidiventris occurs east of the Rift and it is largely replaced by masukuensis on the western plateau, with a few records of pallidiventris from the west (Zobue and

Phirilongwe; Dowsett-Lemaire & Dowsett 2006: 419). *M. r. unasukueusis* occurs in south-east Democratic Republic of Congo (Schouteden 1956).

Field observations

During the 'Filling the Knowledge Gaps Ecological Expedition' to the Itulu Forest Reserves of Tabora Region, western Tanzania, in January 2011, I saw two *M. rufiveutris* ssp. with pale irides among a mixed-species foraging flock in pristine miombo woodland. My field notes are fairly consistent with descriptions of *M. r. pallidiveutris* excluding eye colour and 'a grey band between [the belly] and the black of the head'. Several poorquality photographs show birds fairly typical of *pallidiveutris* except the pale eyes (Fig. 2). Other individuals in the same flock had dark irides. None appeared to be juveniles. My observation occurred *c*.3 months after the known breeding peak (October) for the species in Tanzania (Baker & Baker in prep.). See Table 1.

Subsequently, I contacted S. Stolberger and R. Glen, who provided details of 11 sightings between November 2006 and August 2013 of birds consistent with the then-presumed extralimital race M. r. masukueusis from western Ruaha National Park, Mbeya Region, in western Tanzania. All of these sightings involved birds with pale eyes. M. Baker also provided field records from Tulawaka at the northernmost extreme of the western range of M. r. pallidiveutris. His sightings, in October 2004–November 2011, all involved birds with dark eyes (n = 8), including one carrying food to a nest in October 2007 (Table 1).

TABLE 1
Field records of *Melaniparus rufiventris pallidiventris* from western Tanzania in which eye colour was noted, by S. Stolberger (SS), R. Glen (RG), M. Baker (MB) and the author (JA).

Date	Minimum no. seen	Observers	Locality	Latitude	Longitude	Eye colours
11 Oct 2004	1	MB	Tulawaka	$c.03^{\circ}12'\mathrm{S}$	c.31°32′E	dark
14 Oct 2004	1	MB	Tulawaka	$c.03^{\circ}12'S$	c.31°32′E	dark
6 Nov 2006	1	SS & RG	Ruaha N.P.	$c.07^{\circ}44'\mathrm{S}$	c.34°13′E	pale
27 Jan 2007	1	SS & RG	Ruaha N.P.	$c.07^{\circ}44'S$	c.34°13′E	pale
2 Apr 2007	1	SS & RG	Ruaha N.P.	$c.07^{\circ}44'$ S	c.34°13′E	pale
14 Jul 2007	1	SS & RG	Ruaha N.P.	$c.07^{\circ}46'S$	c.34°10′E	pale
22 Aug 2007	1	SS & RG	Ruaha N.P.	$c.07^{\circ}46'S$	c.34°10′E	pale
23 Oct 2007	1 (at nest)	MB	Tulawaka	c.03°12′S	c.31°32′E	dark
21 Jun 2008	1	SS & RG	Ruaha N.P.	$c.07^{\circ}47'$ S	c.34°12′E	pale
17 Aug 2008	1	SS & RG	Ruaha N.P.	$c.07^{\circ}47'$ S	c.34°08′E	pale
20 Nov 2008	1	MB	Tulawaka	$c.03^{\circ}11'S$	c.31°32′E	dark
20 Nov 2008	1	MB	Tulawaka	$c.03^{\circ}11'S$	c.31°32′E	dark
21 Nov 2008	1	MB	Tulawaka	$c.03^{\circ}11'S$	c.31°32′E	dark
23 Nov 2008	1	MB	Tulawaka	$c.03^{\circ}12'S$	c.31°32′E	dark
17 Dec 2008	1	SS & RG	Ruaha N.P.	$c.07^{\circ}47'$ S	c.34°08′E	pale
10 Aug 2009	1	SS & RG	Ruaha N.P.	$c.07^{\circ}47'$ S	c.34°05′E	pale
11 Aug 2009	1	SS & RG	Ruaha N.P.	$c.07^{\circ}47'$ S	c.34°00′E	pale
27 Jan 2011	3	JA	Itulu Hills	$c.05^{\circ}59'S$	c.33°36′E	pale and dark
23 Nov 2011	1	MB	Tulawaka	$c.03^{\circ}12'S$	c.31°32′E	dark
3 Aug 2013	1	SS & RG	Ruaha N.P.	c.07°47′S	c.34°00′E	pale
17 Aug 2013	2	SS & RG	Ruaha N.P.	$c.07^{\circ}43'$ S	c.34°01′E	pale



Figure 2. Rufous-bellied Tits *Melaniparus rufiventris pallidiventris*, Itulu Hills, western Tanzania, 27 January 2011 (Jason Anderson)

Examination of specimens

Biometrics.—I measured wing chord, tail and bill length, and found that *M. r. masukuensis* averages slightly larger (4%) than *M. r. pallidiventris*, with considerable overlap, and that females of *pallidiventris* and *masukuensis* have on average slightly shorter wings and tail than males (4%), again with considerable overlap, as also found by Harrap & Quinn (1996: 339–341). The four west Tanzanian specimens averaged very slightly smaller than those from eastern Tanzania, and smaller than *masukuensis*, but, given the small sample and the fact that three were females, no significant conclusions can be drawn. The unsexed western specimen (ZMB 34759) was larger than the females, within the expected range for *pallidiventris* and *masukuensis* (wing 81 mm, tail 63 mm, bill 10.3 mm).

TABLE 2
Mensural data (wing, tail and bill) from specimens of *Melaniparus rufiventris pallidiventris* and *M. r. masukuensis* at Natural History Museum, Tring (NHMUK) and Museum für Naturkunde, Berlin (ZMB).

	wing chord (mm)			tail length (mm)			bill to skull (mm)					
	range	mean	s.d.	n	range	mean	s.d.	n	range	mean	s.d.	n
M. r. pallidiventris (eastem Tanzania)	74–85	79.4	2.97	18	57–73	63.3	4.49	19	10.3–12.1	11.2	0.57	19
M. r. pallidiventris (western Tanzania)	75–81	78	2.58	4	60-66	62.5	2.65	4	10.3–11.2	10.7	0.44	4
M. r. masukuensis (Zambia, Malaŵi, Democratic Republic of Congo)	75–87	82.2	3.57	19	62–72	66.7	3.03	19	11.0–12.3	11.8	0.37	19



Figure 3. Rufous-bellied Tits *Melaniparus rufiventris pallidiventris* from western (on left) and eastern (on right) Tanzania (Jason Anderson, © Museum für Naturkunde, Berlin)

Plumage.—Descriptions of M. r. masukneusis and pallidiveutris in the literature indicate significant differences only in underparts plumage. M. r. pallidiventris is described as having 'pale pinkish-buff' (Harrap & Quinn 1996: 339), 'pale, washed-out cinnamon' (Fry et al. 2000: 96) or similar, from the lower breast to the vent, compared to darker 'pinkish-cinnamon' (Harrap & Quinn 1996: 339) in masukueusis. The head and throat are described as black in both taxa, becoming mid grey on the breast, with pallidiventris generally considered paler grey on the breast (e.g. Fry et al. 2000: 96). Some variation has been noted: Harrap & Quinn (1996: 341) stated that Tanzanian pallidiventris 'average greyest (least cinnamon) on the underparts' (i.e. belly) among all pallidiventris populations, and Irwin (1981: 253) mentioned that pallidiventris in Zimbabwe 'appears to be unstable, with the abdomen ranging from pinkish buff to pale vinaceous' (discussed further below). Benson et al. (1971: 206) noted that rufiventris from the eastern plateau of Zambia (near Tanzania) 'generally have the abdomen somewhat paler [than other rufiventris in Zambia], but are nearer to masuknensis than to P. r. pallidiventris'. The sexes are considered identical (e.g. Fry et al. 2000) or very similar, with male underparts possibly averaging a 'slightly richer rufous' (masukueusis) and the 'female's bib averaging slightly browner' (pallidiventris) (Harrap & Quinn 1996: 337–339).

My comparison of the plumage of Tanzanian, Zambian and Malaŵian specimens of pallidiventris and masnknensis revealed the following. (1) Significant individual variation in the extent of the black throat between individuals in both east Tanzanian pallidiventris and masnknensis from Malaŵi and Zambia, but masnknensis generally has a broader grey band between the black throat and rufous underparts than east Tanzanian pallidiventris (on which the black usually extends to the upper, mid or lower breast). Notably, the four west Tanzanian specimens have less black (throat alone) than either east Tanzanian pallidiventris or Zambian masnknensis, and a mid-grey breast. The Leiden specimen has a slightly more extensive black throat than other western birds. Fig. 3 compares west and east Tanzanian specimens in Berlin, and Fig. 4 compares the Leiden western specimen (RMNH.AVES.13 1226) with east Tanzanian specimens.

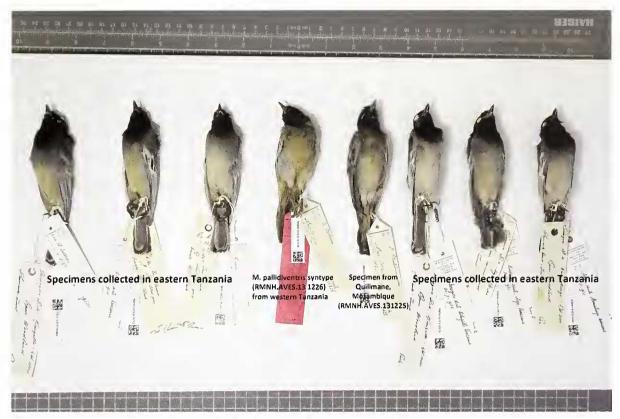


Figure 4. Rufous-bellied Tit *Melaniparus rufiventris pallidiventris* syntype at Naturalis Leiden compared to other *M. r. pallidiventris* skins from eastern Tanzania (© Naturalis Biodiversity Center, Leiden)

- (2) Of the west Tanzanian specimens, the three syntypes collected by Böhm (the southernmost of the western specimens) exhibit the darkest belly, intermediate between east Tanzanian *pallidiventris* and Zambian *masukuensis*. The two northernmost specimens (ZMUC 75.614, ZMB 2000/2138) are paler on the belly, similar to eastern *pallidiventris* (Figs. 3–4).
- (3) No consistent differences were noticed between male and female specimens of any of the taxa within the *rufiventris* complex, *contra* Harrap & Quinn (1996).

Eye colour. – According to the literature (e.g. Harrap & Quinn 1996, Fry et al. 2000), the key difference between pallidiventris and masukuensis is iris colour, documented as brown, dark or dark brown in *pallidiventris* and 'conspicuously yellow' (Harrap & Quinn 1996: 337) or 'pale yellow to brown' (Fry et al. 2000: 96) in masukuensis. The following was noted on specimen labels. (1) Most significantly, of the five west Tanzanian pallidiventris specimens, one of the three syntypes (ZMB 34760, female) had yellow-white ('gelbweiß') eyes. Three (ZMB 34759, ZMB 2000/2138 and ZMUC 75.614) had brown eyes. Eye colour is not known for the Leiden syntype. Eye colour on the 19 eastern Tanzanian specimens was brown (n =2), russet (n = 2), coffee-brown (n = 1), yellow-brownish (gelbbräunlich) (n = 1) or unknown (n = 13). (2) Of the 22 non-Tanzanian adult *pallidiventris* at Tring, eye colour was recorded as sepia (n = 7), brown (n = 2), black (n = 1), 'dark sepia' (n = 1), 'pale burnt umber' (n = 2), light brown (n = 1), pale brown (n = 1: NHMUK 1946.5.766, male, from Kota Kota, central Malaŵi, discussed below), yellow (n = 1: NHMUK 1933.5.11.55, female, from Kazimuli, eastern Zambia, discussed below) or unknown (n = 7). (3) Of the 19 masukuensis specimens at Tring, eye colour was recorded as pale yellow (n = 9), pale ochre-yellow (n = 1), 'pale yellow, outwardly brownish' (n = 1), very pale yellow (n = 1), brown (n = 1: NHMUK 1935.10.9.150, adult female, from Fort Hill, now Chitipa, northern Malaŵi, discussed below), and was unrecorded for six specimens.



Figure 5. Distribution of eye colour and underparts coloration in Rufous-bellied Tits *Melaniparus rufiventris* in western Tanzania, including possible hybridisation zone between *M. r. masukuensis* and *M. r. pallidiventris* (1 = pallidiventris syntypes; 2 = sight records by J. Anderson; 3 = sight records by S. Stolberger & R. Glen; 4 = ZMUC 75.614; 5 = ZMB 2000/2138; 6 = sight records by M. Baker). Grey indicates approximate range of the species in Tanzania.

Discussion

The above records, including field observations and specimen ZMB 34760, confirm the previously undocumented presence of pale-eyed *M. rnfiventris* in western Tanzania, from both Ruaha National Park in Mbeya Region, and Itulu Hills Forest Reserve, Tabora Region, >250 km to the north. Given that the southernmost records in Ruaha National Park are all of pale-eyed birds (best assigned to *masnkuensis*), while the northernmost records all involve dark-eyed birds, and that records from Tabora midway between them are of pale- and dark-eyed individuals (even within the same flock), the presence of a hybrid zone between *pallidiventris* and *masnkuensis* in west-central Tanzania appears probable (see Fig. 5).

Intergradation between masukuensis and pallidiventris has been suggested by several authors, including Benson & White (1957), Benson et al. (1962), Mackworth-Praed & Grant (1963) and Benson & Irwin (1967), who all suggested that intermediates occur in the Zimbabwe / Zambia border region where the two meet. Mackworth-Praed & Grant (1963: 423) also suggested that intermediates occur between nominate rufiventris and 'the Tabora race', i.e. pallidiventris in 'south-eastern Congo', without providing a source for this. The dark-eyed masnkuensis specimen (NHMUK 1935.10.9.150) from Fort Hill in northernmost Malaŵi would also support the hybrid zone theory, if the form in adjacent Tanzania proved to be pallidiventris. Harrap & Quinn (1996: 341) discussed several of the above-mentioned hybrids including the Fort Hill, Kazimuli (NHMUK 1933.5.11.55) and Kota Kota (NHMUK 1946.5.766) specimens; they concluded that 'In all the 'intermediates' seen from Malaŵi or eastern Zambia, the underparts colouration is close to or identical to that of the paler Rufous-bellied Tits found in eastern Zambia, and their status as hybrids appears to rest on eye colouration. As this has clearly been incorrectly noted in some cases, the existence of any hybrids is still to be proven.' My examination of the Fort Hill and Kazimuli specimens is in agreement with Harrap & Quinn (1996) regarding their underparts coloration, but it is also important to note that a 'paler' masukuensis is already intermediate between masukuensis and the rather rufous pallidiventris in southern Malaŵi. Comparison of several individuals of both taxa from Malaŵi, arranged north to south, then across the rift and south again reveals clinal variation in underparts coloration, as Fry et al. (2000) suggested (see Fig. 6). Given that the Kota Kota pallidiventris specimen (NHMUK 1946.5.766, male) is well within the known range of masnknensis (Dowsett-Lemaire & Dowsett 2006) and very similar in underparts coloration to another masukuensis specimen from the same locality, I

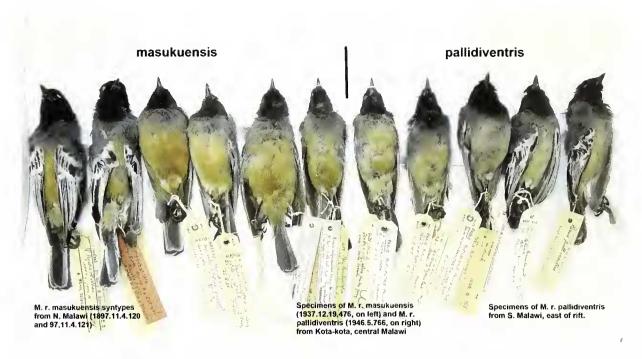


Figure 6. Rufous-bellied Tit *Melaniparus rufiventris masukuensis* and *M. r. pallidiventris* specimens from Malaŵi, showing clinal variation in underparts coloration (Jason Anderson, © Natural History Museum, Tring)

suggest that this individual is best considered as *masukuensis*. Based on locality (Dowsett *et al.* 2008) and iris colour, the Kazimuli specimen (NHMUK 1933.5.11.55, female) is also safely assigned to *masukuensis*.

Alternative explanations for the co-occurrence of pale- and dark-eyed birds within the same population can be tentatively discounted, including the possibility that eye colour variation is sex-related (of the *pallidiventris* syntypes, one female was pale-eyed and two females dark-eyed) or seasonal (Böhm's pale- and dark-eyed syntypes were collected in August 1881, and I recorded pale- and dark-eyed birds together in January 2011). Seasonal movements can also be discounted. Although two references to local movements exist (Mackworth-Praed & Grant 1963: 423, Belcher 1930: 276–277), the vast majority of sources regard *pallidiventris* as sedentary (e.g. Dowsett-Lemaire & Dowsett 2006, Dowsett *et al.* 2008).

The confirmed occurrence of pale- and dark-eyed birds in the same population, even if this is a 'hybrid' form, is notable. Several sources (e.g. Hall 1960, White 1963) have suggested the presence of hybrids between two species fairly closely related to the *rufiventris* complex (Johansson *et al.* 2013), namely pale-eyed White-shouldered Tit *M. guineensis* and dark-eyed White-winged Tit *M. leucomelas* where these two meet (including in south-west Uganda and 'purpurascens' in south-west Ethiopia), although Harrap & Quinn (1996: 324) considered that evidence for hybridisation between them is still lacking.

Taking both iris colour and the degree of rufous in the belly into account, a surprising pattern is apparent among western birds. Those individuals closest to *masukuensis* were all recorded or collected in the southern half of the western range of *pallidiventris*, closer both to the known range of *masukuensis*, as expected, but also, paradoxically, to the only potential interface between western and eastern populations in Tanzania, at the southern end of the Gregory Rift, where stunted miombo may provide a conduit for gene flow between these populations. A specimen from Chimala in this area, in Chicago (FMNH 216938), proved to be an erroneously labelled White-bellied Tit *M. albiventris* (see Fig. 1). Individuals closest in appearance to *pallidiventris* were all from north-west Tanzania (Mgenda, Busondo and

Tulawaka), furthest from eastern *pallidiventris*. This unusual pattern is suggestive of a comparatively recent colonisation event, in which the slightly larger *masuknensis* has moved east from north-east Zambia into south-west Tanzania, breeding with and perhaps partially displacing the smaller *pallidiventris*. This would account for the unstable eye coloration, the slightly darker belly of the more southerly birds and the lack of records of pale-eyed birds in north-west Tanzania.

Aside from eye colour, and the probably clinal degree of rufous saturation on the belly, the comparative lack of black on the breast of west Tanzanian pallidiventris, compared both to east Tanzanian pallidiventris and masukuensis, could signal western birds' distinctiveness from eastern birds or masukuensis. This raises interesting taxonomic questions, given that Reichenow's pallidiventris syntypes were all collected within the suggested hybrid zone. While all three are very slightly paler in belly coloration than north-east Zambian masukuensis, they are also marginally darker than east Tanzanian pallidiventris, which was noticed by Shelley (1900: 240) when he described rovumae (1892, now a synonym of pallidiventris) as having a 'paler buffy white breast' than Reichenow's pallidiventris. If these differences are confirmed in future, resurrection of rovumae for the population east of the central Tanzanian Gregory Rift would be warranted, with differences between the two including the dark brown iris of rovumae compared to unstable eye colour (pale to dark brown) in pallidiventris, black throat and upper breast of rovumae compared to dark grey or black throat and mid-grey breast of pallidiventris, and the slightly richer orange belly of pallidiventris.

Conclusions

The question of whether the *rufiveutris* complex should be treated as two species (Rufous-bellied and Cinnamon-breasted Tits) still requires clarification, although given that the single most distinctive feature used to justify separating them (iris colour) is now known not to be distinctive, and with documentation of a probably hybrid zone, my findings lend support to the opinion that just one species is involved. Clearly, further research is required, including molecular sampling of all populations within *rufiveutris* to clarify levels of divergence between them. In addition, further records from Tanzania west of the Gregory Rift will be instrumental in helping to conclude if east and west Tanzanian forms of *M. r. pallidiveutris* are distinct, thereby justifying recognition of *rovumae*.

Acknowledgements

I thank the sponsors, Condè Nast, and my co-workers on the 'Filling the Knowledge Gaps Ecological Expedition' to western Tanzania in January 2011, Alessandra Soresina, Jo Anderson and Marc Baker, as well as Sue Stolberger and Robert Glen for records, and Anthony Cizek for assistance with maps. For assistance in interpreting molecular data, I thank Ulf Johansson and Rauri Bowie. For assistance with specimens, I thank Mark Adams, Hein von Grouw and Robert Prŷs-Jones at NHMUK, Sylke Frahnert at ZMB, Jon Fjeldså at ZMUC, Steven van der Mije and Rene Dekker at Naturalis (Leiden), Mary Hennen and John Bates at the Field Museum of Natural History (Chicago), Paul Sweet and Selena Flores at the American Museum of Natural History (New York), Rauri Bowie at MVZ, Jeremiah Trimble at MCZ, and Giorgio Chiozzi and all other museum staff who sent data or photographs. For their opinions and assistance with this paper, I am grateful to Neil & Liz Baker, Colin Beale, Anthony Cizek, Guy Kirwan, Kevin McGraw and Don Turner, as well as Bob Dowsett for his detailed constructive criticism of the submitted manuscript.

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